

The effects of wind speed, competition, and body size on perch height selection in a guild of Libellulidae species (Odonata)

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ABSTRACT

For eleven species of sympatric libellulids, male mean mass was positively correlated with wing aspect ratio, wing loading, and mean perch height. We tested the hypotheses that perch height selection was governed by interspecific competition or biomechanical responses to increased wind speed at higher perches. Although larger odonates might prefer higher perches to offset their increased wing loading, species' mean perch height did not correlate with changes in mean or maximum wind speeds. Rather, perch height selection is best explained by competitive interactions. Mean mass (\log_{10} transformed) of these species are distributed in a significantly non-random manner, consistent with community-wide character displacement. Also, observations of aggressive interactions and the response to decoys of three abundant species revealed a competitive hierarchy based on body size. *Libellula luctuosa*, the largest species, avoided stations with conspecific decoys but was attracted to stations with the decoys of two smaller species. *L. incesta* avoided stations with larger *L. luctuosa* decoys, but was attracted to stations with smaller *Pachydiplax longipennis* decoys. *P. longipennis* avoided stations with conspecific and *L. incesta* decoys. *L. luctuosa* was also more successful in displacing perchers (82.4%) than *L. incesta* (68.9%) and *P. longipennis* (46.6%). In pair-wise contrasts, the larger species was always more successful at displacing the smaller species. Finally, *P. longipennis* was attacked at significantly higher rates when it perched on high perches than when it perched at lower perches. We conclude that interspecific competition causes niche partitioning of perch height in this community.

INTRODUCTION

Perch selection by male odonates is an ecologically important behavior that provides access to food and mates (Gorb 1995; Baird & May 1997). In a previous study (Worthen & Jones 2006), we reported that males of ten common libellulid species differ in mean perch height, and mean perch height was positively correlated with a species' mean body size and wind speed in "low perch" (10-40 cm) and "high perch"

(20-80 cm) arrays. Body size was also positively correlated with wing aspect ratio and wing loading. We presented two hypotheses to explain the relationship between body size and perch height: interspecific competition and biomechanical limitation (Worthen & Jones 2006). If high perches are a preferred resource and competitive ability correlates with body size, then the relationship between mean body size and mean perch height could be explained as a competitive hierarchy in which larger species dominate higher perches and displace smaller species to lower perches (as in Rehfeldt & Hadrys 1988; Worthen & Patrick 2004). In addition, competitive interactions among species might result in morphological character displacement. In this case, body sizes would exhibit a non-random, regular distribution indicative of 'limiting similarity' arising from niche partitioning (Hutchinson 1959; Dayan & Simberloff, 2005).

However, because wind speed increases with perch height and wing loading increases with body size (Worthen & Jones 2006), larger species might select higher perches to experience greater headwind speed and generate the compensatory lift necessary to offset their greater wing loading. Smaller species would meet their lift thresholds at lower perch heights. Body size and wing proportions are particularly important for odonates because these characteristics influence critical aspects of flight dynamics such as lift, drag, speed, and maneuverability (Grabow & Ruppell 1995; Norberg 1995; Wakeling 1997; Wakeling & Ellington 1997a-c; Lindhe Norberg 2002). In birds and bats, species differences in body size and wing characteristics correlate with different ecological niches (Fleming 1986; Findley 1993; Landmann & Winding 1993; Norberg 1994; Hertel & Balance 1999). So, the relationship between body size and perch height might be the result of biomechanical limitations rather than competitive interactions between species.

Our goals in this study were to: (1) retest the relationship between perch height selection and morphology in a single experiment with a broad array of perch heights; (2) determine whether species exhibit a regular pattern of body sizes indicative of competitive displacement; (3) reanalyze our 2005 data to test for patterns between perch selection and wind speed; and (4) test for the effects of competitive interactions on perch selection among three of the most common species, *Libellula incesta* Hagen, *L. luctuosa* Burmeister, and *Pachydiplax longipennis* (Burmeister).

MATERIAL AND METHODS

We conducted a survey of perch height preferences of libellulids at a 0.1 ha pond at the Bunched Arrowhead Heritage Trust Preserve (BA), ca 15 km N of Greenville, SC (34°59'34.34"N, 82°22'21.73"W; elevation 303 m). We established four stations, 5 m apart, 50 cm from the shore. At each station, seven wooden dowels (7.5 mm diameter) were placed 10 cm apart, emerging to heights of 3, 10, 20, 40, 60, 80, and 100 cm above the water. Height order was randomized at each station. Observations were made for 1 h on nine dates from 14 June - 9 August 2006. During each observation period, we recorded as many landings and departures as possible, noting the species, perch height, and station. By noting intervening departures, separate perch events could be tallied. Mean perch heights were computed for observations when each species perched alone at a station. These mean perch heights were correlated with the mean mass, fore wing, and hind wing aspect ratios for each species published in Worthen & Jones (2006). We tested the hypothesis that the species in this

community demonstrate ‘limiting similarity’ in body size by subjecting the intervals between \log_{10} transformed mean mass values to a variance analysis (Poole & Rathke 1979; Pleasants 1994; Williams 1995).

To test the hypothesis that these libellulid species alter their perch height based on wind speed, we reanalyzed data from Worthen & Jones (2006). In that study, we observed perching behaviors of ten common libellulid species at five man-made ponds in the piedmont of northwestern South Carolina, USA, in experiments using “low perch” (10, 20, 30, and 40 cm) or “high perch” (20, 40, 60, and 80 cm) arrays (for complete site descriptions, see Worthen & Jones 2006). In both experiments, five perch stations, 5 m apart and 50 cm from the shoreline, were established at each pond. At each perch station, four wooden dowels (7.5 mm diameter) were positioned 10 cm apart; height order was randomized within each station. Each pond was visited at least four times (BA was visited six times) for “low perch” trials and four times for “high perch” trials. A ‘wind station’ was positioned between the second and third perch stations 50 cm from the shore, consisting of four flywheel anemometers (Kestrel® 1000) placed at the same heights as the perches. During the one-hour observation period, we listed as many landings and departures as possible, noting the species, perch height, and station. By noting intervening departures, separate perch events could be tallied. Mean wind speed and maximum wind speeds were recorded after 30 min and 60 min; anemometers were reset after the 30 min recording.

To test the hypothesis that perch height selection is affected by wind speed, we correlated mean perch height of each species during an observation period with mean and maximum wind speed ($\text{m}\cdot\text{s}^{-1}$). We hypothesized that, if species perched at a height that provided a critical amount of headwind for lift, then mean perch height should decline as mean and maximum wind speed increases because the putative critical threshold would occur at a lower height.

We also conducted an experiment to describe the interactive effects of competition and perch height availability on perch height selection by *Libellula incesta*, *L. luctuosa*, and *Pachydiplax longipennis*. Four perching stations were established at Furman Lake, a 12 ha man-made impoundment on the campus of Furman University (34°55′33.48″N, 82°26′27.68″W; elevation 306 m). The stations were 10 m apart, 50 cm from shore. Prior to each 1 h observation period, two stations were randomly assigned to a “uniform height” treatment and received four wooden dowels (7.5 mm diameter), 10 cm apart, that all emerged 100 cm from the water. The other two stations were assigned to a “variable height” treatment and received perches that emerged 100, 40, 60, and 80 cm from the water, in order. In addition, one station of each treatment type received a ‘decoy’ – a preserved specimen of either *L. incesta*, *L. luctuosa*, or *P. longipennis* positioned on its own 100 cm perch, 10 cm behind the first 100 cm perch at that station. This design was repeated in four replicates for each decoy species, twice for 1 h between 10:00 - 12:00 h, and twice for 1 h between 14:00 - 16:00 h. The order of morning and afternoon sampling periods and the species of decoy selected for a given replicate were randomized. Replicates were conducted between 1 August and 30 August 2006. During each one-hour observation period, we listed as many landings and departures as possible, noting the species, perch height, and station. Chi-square tests were used to describe the effects of the presence of decoys and perch-height treatment on the frequency of station use and perch height use within stations of *L. incesta*, *L. luctuosa*, and *P. longipennis*. All analyses were limited to situations where individuals perched alone within a station.

This experimental design allowed us to describe the effect of a decoy at two scales. First, we addressed whether the presence of a decoy affected the selection of perching stations. Second, at a smaller scale, we addressed whether the presence of a decoy influenced perch selection within a station. We measured these effects for different species of decoys, across different types of perching arrays (uniform or variable in height).

We also compared the number and outcome of direct aggressive encounters between these species. First, we compared the frequencies at which the decoys were attacked. Next, we recorded as many interactions between live odonates as possible during the 1 h observation periods, noting the species of attacking and perched individuals and whether the attack resulted in the displacement of the perched individual. To determine whether particular interactions occurred at non-random frequencies, we used Chi-square Goodness of Fit tests to compare the frequency of attacks to the relative abundances of these species in the habitat, as measured by the relative frequencies that species perched alone at stations throughout the experiment. We used Chi-square Tests of Independence to determine whether the success rates of attacks varied among species. These analyses were conducted from two perspectives. For each species, we compared the frequencies at which it attacked the three target species and the frequencies at which it was attacked by the three target species.

We also recorded the perch height for a subset of these encounters. For this haphazard subset, we were able to determine whether attacks fell equally on a species perched at different heights, or if attacks from other species fell differentially across perch heights and encouraged niche partitioning. We used Chi-square Goodness of Fit tests to compare the frequencies of interspecific attacks received by a species at different perch heights with the frequencies expected at random, based on the relative abundance of perch height use by that species when it perched alone.

RESULTS

Species differences in perch height, and relationships with morphology

Males of eleven libellulid species landed on the experimental perches at BA: *Celi-themis elisa* (Hagen), *C. fasciata* Kirby, *C. verna* Pritchard, *Erythemis simplicicollis* (Say), *Libellula auripennis* Burmeister, *L. cyanea* Fabricius, *L. incesta*, *L. luctuosa*, *Pachydiplax longipennis*, *Perithemis tenera* (Say) and *Plathemis lydia* (Drury). Species differed in their perch-height selection (Table 1). *P. tenera* and *E. simplicicollis* preferred low perches, *C. verna* and *P. lydia* preferred intermediate perches (averaging ~ 40 cm), *L. incesta* and *L. luctuosa* preferred the highest perches, and the remaining species used all perches 20-100 cm in height, with mean perch heights between 60-70 cm (Table 1). Mean perch height was significantly correlated with a species' mean mass ($r_s = 0.636$, $p = 0.02$; Fig. 1), mean fore wing aspect ratio ($r_s = 0.691$, $p = 0.01$), and mean hind wing aspect ratio ($r_s = 0.615$, $p = 0.02$); but was not correlated with mean wing loading ($r_s = 0.400$, $p = 0.11$). Mean mass was significantly correlated with fore wing aspect ratio ($r_s = 0.545$, $p = 0.04$), hind wing aspect ratio ($r_s = 0.620$, $p = 0.02$), and wing loading ($r_s = 0.836$, $p = 0.001$; $n = 11$ for all comparisons; one-tailed Spearman rank correlations). The \log_{10} transformed mean mass values of these species are distributed in a significantly non-random, regular distribution ($V = 0.000247$, $p < 0.001$).

Table 1. Frequencies of perch use by male libellulids across seven perch heights (3–100 cm) at Bunched Arrowhead Heritage Preserve, Travelers Rest, South Carolina, USA. Species are listed in order of increasing mean perch height to facilitate comparison. Mean perch height is significantly correlated with mean mass, forewing aspect ratio, and hind wing aspect ratio (see text). *n*: total perch events where individuals perched alone within a station.

Taxon	Perch height [cm]								mean
	<i>n</i>	3	10	20	40	60	80	100	
<i>Perithemis tenera</i>	7	-	7	-	-	-	-	-	10.0
<i>Erythemis simplicicollis</i>	41	-	2	32	7	-	-	-	22.9
<i>Celithemis verna</i>	8	-	-	3	-	5	-	-	45.0
<i>Plathemis lydia</i>	3	-	-	-	2	1	-	-	46.7
<i>Celithemis elisa</i>	1	-	-	-	-	1	-	-	60.0
<i>Celithemis fasciata</i>	37	-	-	1	6	20	6	4	63.2
<i>Libellula auripennis</i>	36	-	-	-	-	30	5	1	63.9
<i>Pachydiplax longipennis</i>	36	-	-	1	9	13	5	8	65.6
<i>Libellula cyanea</i>	5	-	-	-	-	3	2	-	68.0
<i>Libellula incesta</i>	176	-	-	-	-	27	42	107	89.1
<i>Libellula luctuosa</i>	69	-	-	-	-	8	18	43	90.1

Relationships between wind speed and perch height

We reanalyzed our 2005 data and correlated species' mean perch height with mean and maximum wind speeds in "low perch" and "high perch" trials (Table 2). In low perch trials, no species showed the expected decline in mean perch height with increasing mean or maximum wind speed (Table 2). In high perch trials, only the correlation between mean perch height of *P. longipennis* and mean wind speed was statistically significant (Table 2). In total, and without a correction for multiple comparisons, only one of 28 correlations between mean perch height and mean or maximum wind speed was statistically significant (Table 2).

Effects of decoys on perch selection in different perch arrays

The selection of perching stations by *L. incesta* was not affected by the presence of conspecific decoys, either across the entire experiment ($\chi^2 = 0.6$) or within 'uniform' ($\chi^2 = 0.0$) or 'variable' ($\chi^2 = 1.2$) perch treatments (Table 3). Within stations of 'uniform' perches, however, *L. incesta* selected more distant perches when conspecific decoys were present ($\chi^2 = 13.7$, $p < 0.05$; Table 3). Within stations of 'variable' perches, however, the presence of a conspecific decoy had no effect; *L. incesta* preferred the highest perches to a similar degree, whether a decoy was present or not ($\chi^2 = 3.1$; Table 3).

In contrast, *L. incesta* avoided stations with decoys of the larger *L. luctuosa* ($\chi^2 = 6.8$, $p < 0.01$); particularly at 'variable' perch stations where the decoy was behind the only 100 cm perch in the array ($\chi^2 = 6.6$, $p < 0.05$; Table 3). Visits by *L. incesta* to 'uniform' perch stations were depressed by the presence of a *L. luctuosa* decoy, but not to a statistically significant degree ($\chi^2 = 1.0$; Table 3). Again, however, at these 'uniform' stations with multiple 100 cm perches, the presence of a *L. luctuosa* decoy caused *L. incesta* individuals to select more distant perches within the station ($\chi^2 = 15.4$, $p < 0.01$; Table 3).

The effect of *P. longipennis* decoys on *L. incesta* perching behavior was strongly affected by the type of perch array. At 'uniform' stations with multiple high perches, the presence of a *P. longipennis* decoy had no effect on either the selection of perch stations ($\chi^2 = 0.1$) nor the selection of perches within a station ($\chi^2 = 4.1$; Table 3). At stations with 'variable' perch heights, however, the pattern was much different. In fact, the presence of a *P. longipennis* decoy increased the frequency of station use by *L. incesta* ($\chi^2 = 21.1$, $p < 0.01$), and they also used the highest perches directly in front of the decoy to a slightly greater (though statistically insignificant) degree ($\chi^2 = 2.4$; Table 3).

L. luctuosa avoided conspecific decoys at every opportunity, avoiding stations with conspecific decoys in both 'uniform' ($\chi^2 = 9.0$, $p < 0.01$) and 'variable' ($\chi^2 = 19.6$, $p < 0.01$) perch treatments and across the entire experiment ($\chi^2 = 28.4$, $p < 0.01$), and selecting lower perches when decoys were present in 'variable' stations ($\chi^2 = 19.7$,

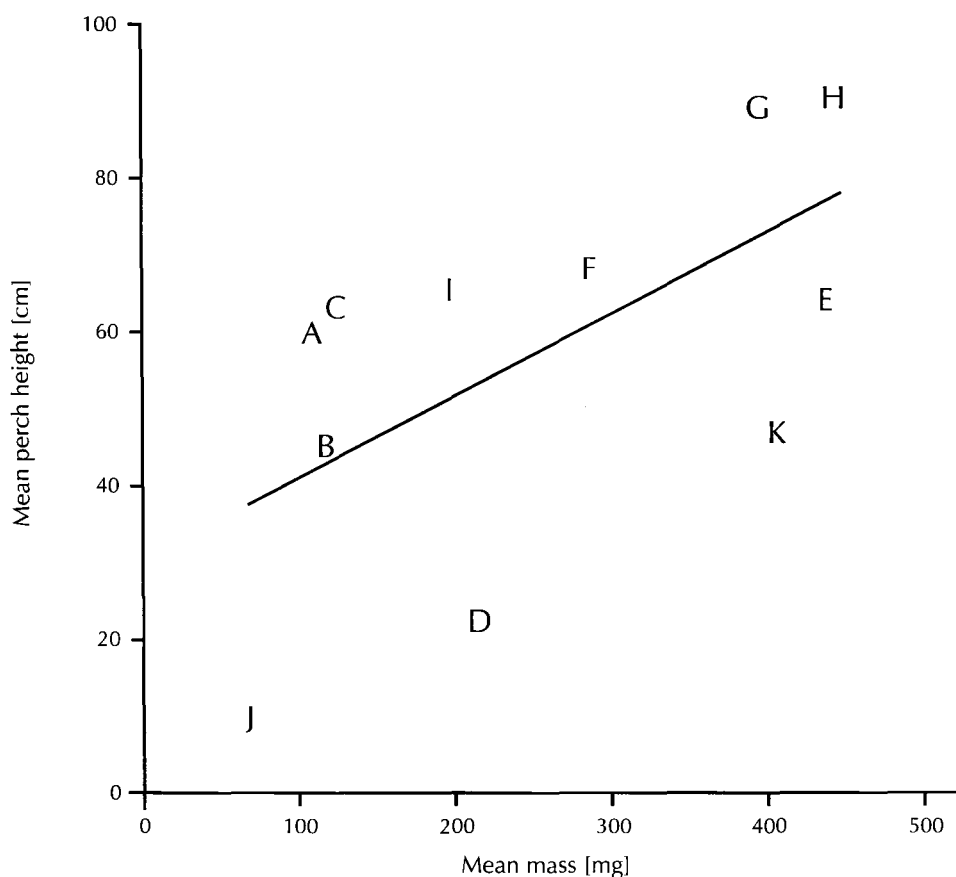


Figure 1: The relationship between the mean mass [mg] of males from 11 common libellulid species and their mean perch height; $r_s = 0.636$, $p = 0.02$, $n = 11$. Mean mass values (\log_{10} transformed) are non-randomly distributed (see text). — A: *Celithemis elisa*; B: *C. verna*; C: *C. fasciata*; D: *Erythemis simplicicollis*; E: *Libellula auripennis*; F: *L. cyanea*; G: *L. incesta*; H: *L. luctuosa*; I: *Pachydiplax longipennis*; J: *Perithemis tenera*; K: *Plathemis lydia*.

Table 2. Spearman Rank correlations between mean perch height and wind speed for ten common libellulid species. Experiments were conducted in "low perch" (10-40 cm) and "high perch" (20-80 cm) trials at five ponds in South Carolina, USA, in 2005. Mean: mean wind speed [$\text{m}\cdot\text{s}^{-1}$]; Max: maximum wind speed [$\text{m}\cdot\text{s}^{-1}$]; n : number of observation periods; n.s.: not significant; *: $p < 0.05$; †: no variation in one variable; correlation could not be computed.

Taxon	Low perch			High perch		
	n	Mean	Max	n	Mean	Max
<i>Perithemis tenera</i>	7	-0.101 n.s.	0.091 n.s.	1	-	-
<i>Celithemis fasciata</i>	4	-0.316 n.s.	0.738 n.s.	5	-0.400 n.s.	-0.500 n.s.
<i>Pachydiplax longipennis</i>	19	-0.070 n.s.	-0.227 n.s.	14	-0.612 *	-0.311 n.s.
<i>Erythemis simplicicollis</i>	10	-0.139 n.s.	-0.248 n.s.	9	0.277 n.s.	0.292 n.s.
<i>Libellula cyanea</i>	3	-0.866 n.s.	-0.866 n.s.	2	-	-
<i>Libellula incesta</i>	14	0.508 n.s.	0.424 n.s.	18	-0.054 n.s.	-0.131 n.s.
<i>Plathemis lydia</i>	10	0.123 n.s.	0.222 n.s.	5	0.224 n.s.	-0.224 n.s.
<i>Libellula auripennis</i>	1	-	-	3	-†	-†
<i>Libellula luctuosa</i>	3	0.000 n.s.	-0.866 n.s.	9	0.000 n.s.	-0.252 n.s.
<i>Libellula vibrans</i>	0	-	-	2	-	-

$p < 0.01$; Table 3). In contrast, *L. luctuosa* were attracted to stations with decoys of *P. longipennis* ($\chi^2 = 11.0$, $p < 0.01$) or *L. incesta* ($\chi^2 = 18.0$, $p < 0.01$; Table 3). *L. luctuosa* were particularly attracted to stations with *P. longipennis* decoys in the 'variable' arrays with only a single high perch ($\chi^2 = 12.3$, $p < 0.01$), but were attracted to *L. incesta* decoys at the 'uniform' stations ($\chi^2 = 21.4$, $p < 0.01$; Table 3). However, neither *L. incesta* decoys nor *P. longipennis* decoys affected the distribution of perch choice by *L. luctuosa* within stations (Table 3).

P. longipennis avoided stations with conspecific decoys ($\chi^2 = 21.3$, $p < 0.01$) and *L. incesta* decoys ($\chi^2 = 21.2$, $p < 0.01$), particularly in 'uniform' perch arrays (*P. longipennis* decoys: $\chi^2 = 15.0$, $p < 0.01$; *L. incesta* decoys: $\chi^2 = 41.0$, $p < 0.01$; Table 3). They also shifted away from conspecific decoys in 'uniform' arrays ($\chi^2 = 33.9$, $p < 0.01$), and away from *L. incesta* decoys in 'variable' arrays ($\chi^2 = 10.9$, $p < 0.05$; Table 3). Curiously, there was no evidence of any effect of *L. luctuosa* decoys on *P. longipennis* behavior at either the 'between station' or 'within station' scales (Table 3).

To summarize, *L. incesta* tended to avoid 'variable' perch stations when *L. luctuosa* decoys were present, but increased visitation to 'variable' perch stations when *P. longipennis* decoys were present. When multiple high perches were available in the 'uniform' treatments, *L. incesta* did not avoid stations with decoys, but did shift away from both *L. incesta* and *L. luctuosa* decoys to more distant perches. *L. luctuosa* avoided conspecific decoys at both the between station and within station scales. However, *L. luctuosa* was attracted to perch stations that had decoys of the other two species present. *P. longipennis* avoided stations with conspecifics and *L. incesta*, and shifted away from these species in 'uniform' and 'variable' arrays, respectively. There were no statistically significant effects of *L. luctuosa* decoys on *P. longipennis*.

Table 3a. Frequency of perch events by *Libellula incesa*, *L. luctuosa*, and *Pachydiplax longipennis*, at stations with uniform perches, in the presence (P) or absence (A) of a decoy. Chi-square values beneath a decoy name compare total perches in the presence or absence of that decoy, pooled across uniform and variable perch treatments. Chi-square values beneath a table compare total perches in the presence or absence of that decoy in uniform perch treatments. Chi-square values in columns at the end of the table compare the distribution of perches used in the presence or absence of a decoy within that perch treatment (**bold** = significant avoidance of a decoy, $p < 0.05$; **bold italics** = significant attraction to a decoy, $p < 0.05$). Tot: total perches in the presence or absence of a decoy in that perch treatment.

Decoy		Uniform Perch Heights (cm)					
		100	100	100	100	Tot	χ^2
<i>L. incesa</i> perches:							
<i>L. incesa</i>	P	11	9	13	34	67	13.7
$\chi^2 = 0.6$	A	30	7	10	19	66	
						$\chi^2 = 0.0$	
<i>L. luctuosa</i>	P	8	5	14	30	57	15.4
$\chi^2 = 6.8$	A	26	13	10	19	68	
						$\chi^2 = 1.0$	
<i>P. longipennis</i>	P	20	17	20	27	84	4.1
$\chi^2 = 9.5$	A	30	14	13	32	89	
						$\chi^2 = 0.1$	
<i>L. luctuosa</i> perches:							
<i>L. incesa</i>	P	11	12	5	16	44	4.9
$\chi^2 = 18.0$	A	2	2	4	2	10	
						$\chi^2 = 21.4$	
<i>L. luctuosa</i>	P	0	0	0	0	0	-
$\chi^2 = 28.4$	A	5	2	2	0	9	
						$\chi^2 = 9.0$	
<i>P. longipennis</i>	P	1	4	2	11	18	6.4
$\chi^2 = 11.0$	A	4	1	2	3	10	
						$\chi^2 = 2.3$	
<i>P. longipennis</i> perches:							
<i>L. incesa</i>	P	3	3	2	4	12	0.9
$\chi^2 = 21.2$	A	26	16	12	16	70	
						$\chi^2 = 41.0$	
<i>L. luctuosa</i>	P	4	4	3	8	19	1.1
$\chi^2 = 2.5$	A	6	2	3	8	19	
						$\chi^2 = 0.0$	
<i>P. longipennis</i>	P	1	2	5	32	40	33.9
$\chi^2 = 21.3$	A	32	13	16	22	83	
						$\chi^2 = 15.0$	

Table 3b. Frequency of perch events by *Libellula incesa*, *L. luctuosa*, and *Pachydiplax longipennis*, at stations with variable perches, in the presence (P) or absence (A) of a decoy. Chi-square values beneath a table compare total perches in the presence or absence of that decoy in variable perch treatments. Chi-square values in columns at the end of the table compare the distribution of perches used in the presence or absence of a decoy within variable perch treatments (**bold** = significant avoidance of a decoy, $p < 0.05$; **bold italics** = significant attraction to a decoy, $p < 0.05$). Tot: total perches in the presence or absence of a decoy in that perch treatment.

Decoy		Variable Perch Heights (cm)				Tot	χ^2
		100	40	60	80		
<i>L. incesa</i> perches:							
<i>L. incesa</i>	P	50	0	1	34	85	3.1
	A	46	0	1	53	100	
						$\chi^2 = 1.2$	
<i>L. luctuosa</i>	P	34	0	2	40	76	0.8
	A	52	1	3	55	111	
						$\chi^2 = 6.6$	
<i>P. longipennis</i>	P	60	0	4	65	129	2.4
	A	24	0	1	40	65	
						$\chi^2 = 21.1$	
<i>L. luctuosa</i> perches:							
<i>L. incesa</i>	P	2	0	2	4	8	2.4
	A	2	0	0	6	8	
						$\chi^2 = 0.0$	
<i>L. luctuosa</i>	P	1	1	0	0	2	19.7
	A	1	0	5	19	25	
						$\chi^2 = 19.6$	
<i>P. longipennis</i>	P	2	0	6	7	15	1.4
	A	0	0	1	0	1	
						$\chi^2 = 12.3$	
<i>P. longipennis</i> perches:							
<i>L. incesa</i>	P	0	3	12	19	34	10.9
	A	7	6	8	11	32	
						$\chi^2 = 0.1$	
<i>L. luctuosa</i>	P	6	9	14	21	50	1.9
	A	7	20	19	24	70	
						$\chi^2 = 3.3$	
<i>P. longipennis</i>	P	15	6	14	31	66	2.5
	A	25	8	22	29	84	
						$\chi^2 = 2.1$	

Table 4. Percentages of attacks that successfully displaced a percher during interactions between *Libellula incesa*, *L. luctuosa*, and *Pachydiplax longipennis*. Total number of attacks are in parentheses. χ^2 TI-P and χ^2 TI-A: Chi-square Test of Independence values comparing the rates of successful attacks on a species and by a species, respectively. χ^2 GF-P and χ^2 GF-A: Chi-square Goodness of Fit values comparing the frequency of attacks on a species and by a species, respectively, with the frequency of these species at the study site (see text). *: $p < 0.05$; **: $p < 0.01$.

Perched species	Attacking species			χ^2 TI-P	χ^2 GF-P
	<i>L. incesa</i>	<i>L. luctuosa</i>	<i>P. longipennis</i>		
<i>L. incesa</i>	88.2 (17)	87.5 (16)	44.6 (74)	17.55 **	79.32**
<i>L. luctuosa</i>	50.0 (20)	100.0 (2)	63.6 (11)	2.11 n.s.	0.36 n.s.
<i>P. longipennis</i>	69.1 (175)	75.0 (16)	45.8 (48)	9.75 *	23.04**
χ^2 TI-A	6.30 *	1.32 n.s.	1.41 n.s.		
χ^2 GF-A	249.06 **	3.11 n.s.	0.59 n.s.		

Patterns of aggressive interactions among species

Decoys were attacked 77 times throughout the experiment, with more attacks falling on *P. longipennis* decoys (55/77 = 67.5%) than the decoys of *L. incesa* (22/77 = 28.6%) or *L. luctuosa* (3/77 = 3.9%). These frequencies of attack were significantly different from the relative frequency of decoys (χ^2 Goodness of Fit = 47.58, $p < 0.01$) or the relative distribution of these species at the study sites (33%, 58%, and 9%, respectively; χ^2 Goodness of Fit = 41.55, $p < 0.01$).

Table 5. Percentage of interspecific attacks received by *Libellula incesa*, *L. luctuosa*, and *Pachydiplax longipennis* across different perch heights, compared to percentages expected based on the relative frequencies of perch-height use (χ^2 Goodness of Fit, **: $p < 0.01$). 100⁺: includes perches from 'variable height' and 'uniform height' stations. n: sample size.

		Perch height [cm]				n	χ^2
		40	60	80	100 ⁺		
<i>L. incesa</i>	% observed	0.0	0.0	35.9	64.1	64	
	% expected	0.1	1.2	28.8	69.9	997	2.28 n.s.
<i>L. luctuosa</i>	% observed	0.0	0.7	43.8	56.2	16	
	% expected	0.0	9.0	24.0	66.0	150	4.43 n.s.
<i>P. longipennis</i>	% observed	1.5	3.8	35.9	58.8	131	
	% expected	9.0	15.4	23.3	52.3	579	29.39 **

In general, *L. incesa*, *L. luctuosa*, and *P. longipennis* were equally aggressive; the proportion of attacks made by each species (56%, 9%, and 35%, respectively) were consistent with their relative abundances in the environment (58%, 9%, and 33%, respectively; χ^2 Goodness of Fit = 0.78, n.s.). However, *L. incesa* attacked perched species non-randomly (χ^2 Goodness of Fit = 249.06, $p < 0.01$; Table 4), attacking *P. longipennis* 82.5% of the time, far in excess of the relative abundance of *P. longipennis* (33%). *L. incesa* also varied in their success rates when they attacked different species, with better success displacing conspecifics and *P. longipennis* than *L. luctuosa* (χ^2 Test of Independence = 6.30, $p < 0.05$, Table 4). In contrast, *L. luctuosa* and *P. longipennis* attacked perched species at random, at the same frequency that they occurred at the study site (χ^2 Goodness of Fit tests were not significant; Table 4). In addition, neither species varied in their success at displacing perched species (χ^2 Tests of Independence were not significant; Table 4). However, *L. luctuosa* was far more successful in displacing perched libellulids (total success rate = $28/34 = 82.4\%$) than *L. incesa* (total success rate = $146/212 = 68.9\%$) and *P. longipennis* (total success rate = $62/133 = 46.6\%$; χ^2 Test of Independence = 23.63, $p < 0.01$).

As perched targets, species were not attacked at rates equal to their relative frequency in the habitat (χ^2 Goodness of Fit = 161.72, $p < 0.01$). Rather, *P. longipennis* was a more frequent victim ($239/379 = 63\%$) than its relative abundance in the habitat would dictate (33%), and *L. incesa* was a less frequent victim ($107/239 = 28\%$) than its relative abundance would dictate (58%). When *L. incesa* was attacked, those attacks were disproportionately made by *P. longipennis* (χ^2 Goodness of Fit = 79.32, $p < 0.01$; Table 4). Likewise, when *P. longipennis* was attacked, the attacks were disproportionately made by *L. incesa* (χ^2 Goodness of Fit = 23.04, $p < 0.01$; Table 4). *L. luctuosa*, however, was attacked by species at the same relative frequencies as attacking species occurred in the habitat (χ^2 Goodness of Fit test was not significant; Table 4). Species were also displaced at different rates by different attacking species. *P. longipennis* was more readily displaced by *L. incesa* and *L. luctuosa* than by conspecifics (χ^2 Tests of Independence = 9.75, $p < 0.05$; Table 4). *L. incesa* was displaced more successfully by conspecifics and *L. luctuosa* than by *P. longipennis* (χ^2 Tests of Independence = 17.55, $p < 0.01$; Table 4). *L. luctuosa* was more easily displaced by conspecifics than by *L. incesa* or *P. longipennis*, though not to a statistically significant degree (χ^2 Tests of Independence = 2.11; Table 4).

L. incesa and *L. luctuosa* perched most often on the highest perches (69.9% and 66.0%, respectively, Table 5). So, if these species were attacked at random across perch heights, then 69.9% and 66.0% of interspecific attacks should fall on these species at this height. However, both species receive fewer interspecific attacks at this height than expected (by 5% and 10%, respectively), though not to a statistically significant degree (Table 5). In contrast, *P. longipennis* was attacked at a significantly greater frequency at high perches than expected. It used 80cm and 100cm perches 75.5% of the time, but received 93.7% of its interspecific attacks at these heights (χ^2 Goodness of Fit = 29.39, $p < 0.01$; Table 5). Including intraspecific attacks did not change these patterns; *L. incesa* and *L. luctuosa* experienced fewer attacks than expected at the highest perches, though not to a statistically significant degree, and *P. longipennis* experienced fewer attacks than expected at low heights and more attacks than expected at high heights (χ^2 Goodness of Fit = 25.00, $p < 0.01$).

DISCUSSION

The mean perch height of males of eleven libellulid species was significantly correlated with mean mass, fore wing aspect ratio, and hind wing aspect ratio, confirming the patterns documented in our previous study (Worthen & Jones 2006). The composition of this community differed slightly from our 2005 study, with the addition of *Celithemis elisa* and *C. verna* and the absence of *Libellula vibrans*. However, there were statistically significant correlations between the rank order of species perch heights in this study with the rank order of species perch heights in the “low perch” ($r_s = 0.695$, $p = 0.04$, $n = 9$) and “high perch” ($r_s = 0.746$, $p = 0.04$, $n = 9$) arrays of our previous study (Worthen & Jones 2006). Thus, there is a consistent and repeatable pattern in this community: perch height correlates with body size. However, there are a number of interesting anomalies. For example, *Erythemis simplicicollis*, *L. auripennis*, *Plathemis lydia*, and *Perithemis tenera* perched lower than their body mass would dictate. The low perching of *P. tenera* may be a consequence of its competitive displacement from higher perches (Worthen & Patrick 2005), and the low perching of *E. simplicicollis* and *P. lydia* is consistent with their frequent perching on the ground and other horizontal surfaces. However, the relatively low perching of *L. auripennis* in this study is rather curious, as it was the highest percher in our previous study, always selecting the tallest perch in the array in 33 observations (Worthen & Jones 2006). In addition, *Celithemis* spp. seem to perch higher than their mass would dictate. These patterns suggests that there may be different guilds within this community.

There are several potential explanations for these relationships between body size, flight morphology, and perch height. We tested the hypotheses that these relationships were related to wind speed or competition. Wind speed may be important because of the allometric relationships between body mass and wing shape. Wing loading (force per unit surface area) increases with body size, so large organisms must create greater lift to offset this increased wing loading. One way this can be accomplished is by flying faster, which is facilitated by having narrower wings that produce less drag. Larger dragonflies do fly faster than small dragonflies (Rüppell 1989), and May (1981) reported that ‘fliers’ tended to have narrower wings than ‘perchers’ of the same body size (but see Wakeling 1997). However, because wind speed increases with perch height (Worthen & Jones 2006), another way that large perching dragonflies can offset increased wing loading is to perch on higher perches that provide greater headwind speed. If wind speed determines the relationship between body size and perch height, then individuals of a species could perch at lower heights in stiffer winds and still meet their critical lift threshold. As such, we would expect species to exhibit a negative correlation between their perch height and wind speed. However, when we reanalyzed relationships between perch height and wind speed for 8 species in low and high perch arrays, only one of the 28 correlations between mean perch height and mean and maximum wind speed was statistically significant. As such, we conclude that these species do not select perch heights based on simple relationships between wing morphology and wind speed.

We also tested the hypothesis that perch selection is determined by interspecific competition. First, the regular, non-random distribution of species mean mass va-

lues indicates that this community is structured by interspecific competition at some level. Ever since Hutchinson's (1959) seminal paper, ecologists have appreciated that 'community-wide character displacement' (Strong et al. 1979) is a hallmark of niche partitioning produced by interspecific competition (Simberloff & Boecklin 1981; Dayan & Simberloff 1998). However, although this pattern provides evidence for the 'ghost of competition past' (Connell 1980), it is difficult to determine the limiting resource that drives this difference in body size. Most cases of community-wide character displacement have described differences in trophic structures of carnivores, probably because carnivores can easily partition different sized prey (for reviews, see Dayan & Simberloff 1998, 2005). It is possible that differences in dragonfly body size correlate with differences in prey size or affect perch fidelity. *P. longipennis* feeds on smaller prey and defends territories more aggressively than *E. simplicicollis*, and May & Baird (2002) hypothesize that there may be an energetic explanation for this correlation. It is also possible that differences in adult body size are a consequence of niche partitioning and community-wide character displacement at the larval stage. Large larvae forage disproportionately on large prey (Dillon 1985), and dietary niche shifts occur in the presence of interspecific competitors (Mahato & Johnson 1991). In addition, competitive hierarchies are reinforced by intraguild predation of large larvae on small larvae (Benke 1978; Johnson et al. 1985; Robinson & Wellborn 1987).

Regardless of the cause, body size differences play an important role in perch competition in this guild. *L. luctuosa* is the largest species in the community, and it should be the competitive dominant. It is an aggressive species that often chases other species from its territory (Campanella 1975; Moore 1987). In the decoy experiment, *L. luctuosa* was only discouraged from perching at a station by the presence of a conspecific. The presence of *L. incesa* and *P. longipennis* decoys actually attracted *L. luctuosa* to a station – much as we might expect of a competitively dominant species defending a territory against incursions from competitive subordinates. Also, *L. luctuosa* decoys were only attacked 3 times throughout the entire experiment, significantly less frequently than attacks on the other species' decoys. *L. incesa* exhibits an intermediate position in the competitive hierarchy, consistent with its intermediate size. *L. incesa* avoids stations with the larger, competitively superior *L. luctuosa*, but is attracted to stations with the smaller, subordinate *P. longipennis*. When it did perch in the presence of a *L. luctuosa* decoy, it shifted to a more distant perch.

P. longipennis was the smallest species and was the competitive subordinate. *P. longipennis* decoys and live individuals were attacked significantly more frequently than their relative abundances would dictate. Most attacks were made by *L. incesa* – its immediate neighbor in the competitive size hierarchy. Results from the decoy experiments are less dramatic, but still consistent with its competitive inferiority. *P. longipennis* avoided stations with conspecific and *L. incesa* decoys at uniform arrays. *P. longipennis* showed no avoidance for any decoys in variable arrays, but it shifted to lower perches in the presence of *L. incesa* decoys. The failure to avoid decoys at variable arrays may be a function of the lower mean perch height of *P. longipennis*. Because *P. longipennis* prefers perches in the 60–80 cm range, a decoy placed behind the 100 cm perch may not represent a significant threat. *P. longipennis* can

perch on the 60 cm or 80 cm perch and partition the resource. We might expect a competitive release in the absence of a decoy. However, *P. longipennis* may learn to perch low regardless of immediate neighbors at any particular moment; it suffered most of its attacks when it used high perches and displaced individuals would tend to accumulate on lower perches. The competitive hierarchy was most evident in direct attacks. *L. luctuosa* successfully displaced *L. incesa* and *P. longipennis*, and *L. incesa* successfully displaced *P. longipennis*, all at higher rates than the reciprocal encounters.

In conclusion, the importance of competition in structuring this community is strongly suggested by the non-random community-wide character displacement in body size. These differences in body size correlate with mean perch height, and predict success in interspecific competition for perches among *L. luctuosa*, *L. incesa*, and *P. longipennis*. Coupled with previous research demonstrating that *P. longipennis* drives the smaller *Perithemis tenera* to low perches (Worthen & Patrick 2004), there is growing evidence that competitive hierarchies correlating with body size cause resource partitioning based on perch height. However, whether competition for perch height contributes to the community-wide displacement in body size is unknown.

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